

EFFECTS OF LONG-TERM FOREST CLEAR-CUTTING ON WINTERING AND BREEDING BIRDS

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ABSTRACT.—I examined the effects of even-aged clear-cutting (third cutting cycle) on wintering and breeding bird communities at the Barrens Grouse Habitat Management Area (HMA) in central Pennsylvania, 1987–1989. I tested the hypotheses that community structure and population abundance of wintering and breeding birds did not differ (1) among areas of the Barrens Grouse HMA that varied in extent of clear-cutting (0%, 50%, and 75% areas) or (2) among habitats of different age since clear-cutting on the treated sector (50% and 75% areas). These findings were compared to those obtained subsequent to a second cutting cycle. Abundance of 11 species of wintering birds did not vary ($P > 0.05$) among the three areas. Species richness of all species combined and of ground-shrub foragers was high in the 50% and 75% areas after the third cycle, largely because of additional brushy vegetation. Abundances of all species combined and of ground-shrub foragers were greater than expected in the 75% area but lower than expected in the 0% and 50% areas; abundance of sallier-canopy foragers was greater than expected in the 0% area and less in the 75% area. Two Neotropical migrants, Ovenbird (*Seiurus aurocapillus*) and Red-eyed Vireo (*Vireo olivaceus*), were more sensitive than other area-dependent species to increased fragmentation via forest clear-cutting resulting from the third cycle. I conclude that the creation of a mosaic of small (1 ha), even-aged stands for management of Ruffed Grouse (*Bonasa umbellus*) habitat does not have a detrimental long-term effect on most species of breeding and wintering forest birds on a localized basis. Received 6 July 1992, accepted 9 Nov. 1992.

Forest management for Ruffed Grouse (*Bonasa umbellus*) habitat in central Pennsylvania (Barrens Grouse Habitat Management Area) using an even-aged system of clear-cutting has created a mosaic of small (1 ha) different-aged forest stands (Yahner 1992). Previous studies of avian communities associated with the Barrens Grouse HMA have examined community structure of and habitat use by wintering and breeding bird communities subsequent to a second cutting cycle (Yahner 1984, 1985, 1986, 1987). Since these studies have been conducted, however, a third cutting cycle has been completed at the Barrens Grouse HMA. Hence, this site provided an ideal opportunity to assess the impact of an increase in forest clear-cutting on forest bird communities (Saunders et al. 1991). Such studies are timely because of the concern over the effects of forest management and fragmentation on long-term trends in avifaunal abundance and distribution (e.g., Whitcomb et al. 1981, Robbins et al. 1989).

In this study, I tested the hypotheses that community structure (species composition and diversity) and population abundance of wintering and breeding birds did not differ (1) among three areas of the Barrens Grouse

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HMA that varied in extent of forest clear-cutting, nor (2) among eight habitats of different age since clear-cutting on a treated sector of the Barrens Grouse HMA. These findings were then compared to those obtained in previous studies (Yahner 1984, 1985, 1986, 1987) that examined wintering and breeding bird communities subsequent to a second cutting cycle when the extent of forest clear-cutting was appreciably less.

STUDY AREA

I conducted the study at the 1166-ha Barrens Grouse HMA, State Game Lands 176, Centre County, Pennsylvania, from May 1987 through July 1989. The Barrens Grouse HMA consisted of a reference (control) and a treated (clear-cut) sector of comparable size (Fig. 1). Forest on the reference sector, termed the 0% area of forest clear-cutting, and forest contiguous to the boundaries of the Barrens Grouse HMA had not been clear-cut for about 65 years. The treated sector was comprised of two areas of forest clear-cutting, 50% and 75%. These percentages represented the amount of cut forest in each area after the third cutting cycle (winters 1985–1986 and 1986–1987) using an even-aged system of forest clear-cutting under the supervision of the Pennsylvania Game Commission (PGC). The 50% and the 75% areas were designated by the PGC as primarily mixed-oak (*Quercus* spp.) and aspen (*Populus* spp.) cover types, respectively (Yahner 1986, 1987), but these areas were a combination of both cover types (Yahner and Grimm 1984).

Principal overstory trees (woody stem >7.5 cm dbh and >1.5 m tall) at the Barrens Grouse HMA were bigtooth aspen (*Populus grandidentata*), quaking aspen (*P. tremuloides*), pitch pine (*Pinus rigida*), white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), and red maple (*Acer rubrum*). Major understory trees (woody stem = 2.5–7.5 cm dbh and >1.5 m tall) and tall shrubs (woody stems < 2.5 cm dbh, >1.5 m tall) were aspen (*Populus* spp.), red maple, black cherry (*Prunus serotina*), and oak (*Quercus* spp.), particularly scrub (*Q. ilicifolia*) and dwarf chinkapin oaks (*Q. prinoides*) (Yahner 1987).

The treated sector contained 136 contiguous, 4-ha blocks, each representing a theoretical “activity center” for Ruffed Grouse (Gullion 1977). Seventy-six and 60 blocks were in 50% and 75% areas, respectively (Fig. 1). Each block was subdivided into four 1-ha (100- × 100-m) plots (A–D) and was clear-cut using a clockwise rotation of 40 years (approximate 10-yr cutting cycle) in the 50% area and 20 years (approximate 5-yr cutting cycle) in the 75% area (Yahner 1992). During the winter of 1976–1977 (first cutting cycle), plot A (western plot) of all blocks in both 50% and 75% areas was clear-cut. During the winter of 1980–1981 (second cutting cycle), plot B (northern plot) of blocks in the 75% areas was clear-cut (termed 8-year-old aspen habitat). During the winters of 1985–1986 and 1986–1987 (third cutting cycle), plot B in the 50% area and plot C (eastern plot) in the 75% area were clear-cut (termed 2-year-old oak and 2-year-old aspen habitats, respectively). In the 75% area, plot D (southern plot) remained uncut (termed uncut oak bordered by younger clear-cut plots and uncut oak bordered by older clear-cut plots, respectively). Hence, after the third cycle, clear-cutting in the 50% area consisted of alternating strips of cut plots (A and B) and uncut plots (C and D). In contrast, clear-cutting in the 75% area gave a checkerboard pattern of cut plots (A–C) and uncut plots (D). Uncut oak bordered by younger versus older clear-cut plots in the 50% area were considered distinct from one another because age of proximal clear-cut plots differed and because density of vegetative cover (>2 m of ground level) at interfaces with clear-cut plots varied, being more dense in older than in younger clear-cut plots ($P < 0.05$) (Yahner et al. 1989). Thus, based on the three cutting cycles, I classified

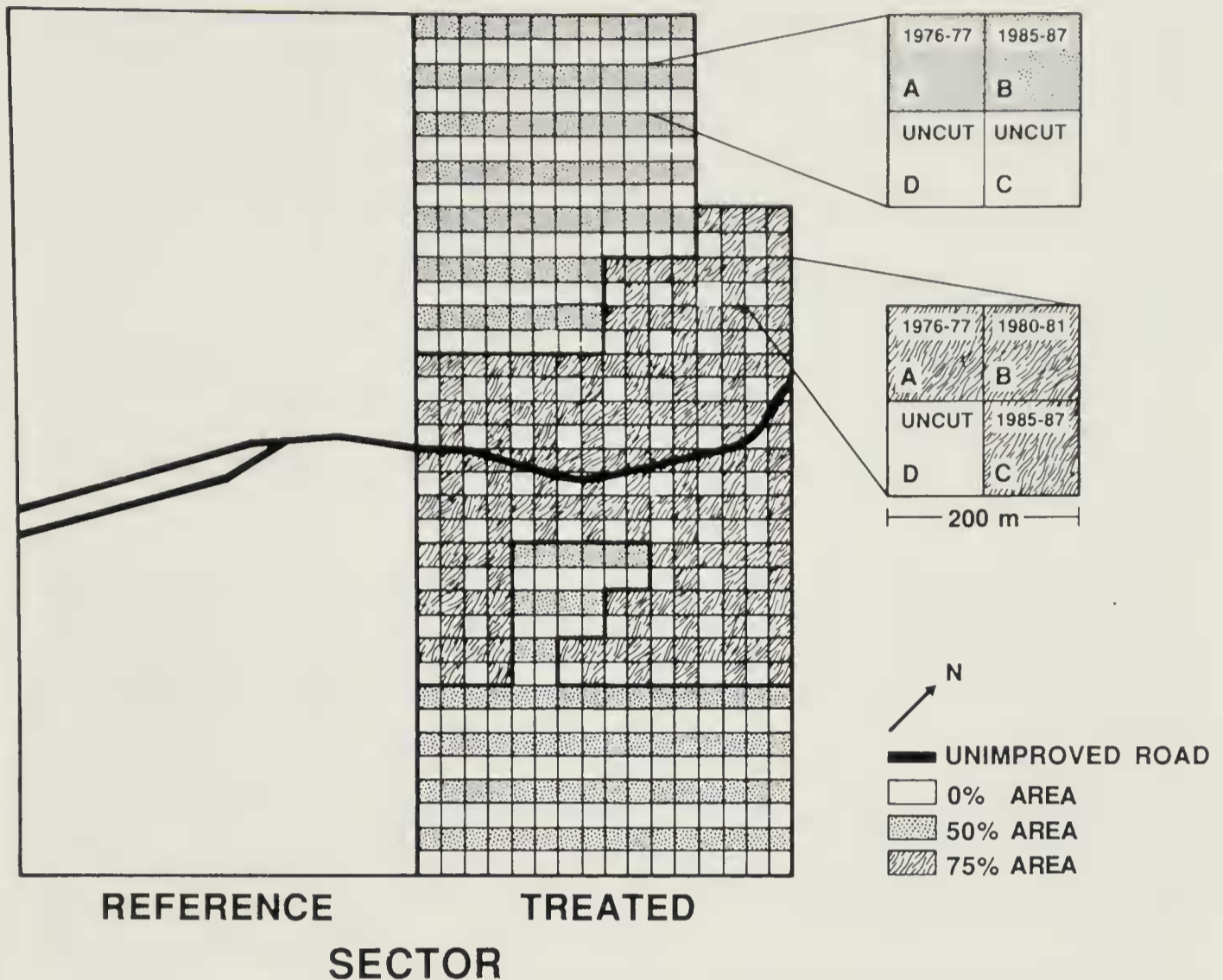


FIG. 1. Schematic of reference and treated sectors at the Barrens Grouse HMA, Centre County, Pennsylvania. Dates of cutting cycles are given in plots A and B of the 76 blocks in the 50% area of forest clear-cutting and in plots A–C of the 60 blocks in the 75% area of clear-cutting. Forest in the 0% area of clear-cutting (reference sector), in plots C and D of the 50% area, and in plot D of the 75% area was uncut.

the Barrens Grouse HMA into nine habitats: uncut habitat on the reference sector and four habitats each (plots A–D) in 50% and 75% areas on the treated sector.

METHODS

I randomly selected ten 1-ha plots on the reference sector and ten plots each in the eight habitats on the treated sector for study, giving ten, 40, and 40 plots, respectively, in the 0%, 50%, and 75% areas. Plots were representative of vegetation in each area and were >50 m from disturbances, e.g., restricted access roads. The minimum distance between plots was 200 m (DeSante 1986).

I visited each plot once from late December to early February in each of two consecutive winters (1987–1988 and 1988–1989) and once again from late May to late June in each of three consecutive breeding seasons (1987–1989). Visits were made between sunrise and 10:30 h DST, and the order of visits was randomized. At each visit, I allowed a 1-min equilibrium period to elapse; then during a subsequent 5-min period, all birds seen or heard were counted within a 30-m radius of the center of the plot (DeSante 1986, Morrison et al. 1986). A 30-m radius circle positioned at the center of a plot was used to minimize edge

effects at interfaces of plots of different age on the treated sector (after Repenning and Labisky 1985). Birds flying through or above the canopy were not counted. Movements of birds were monitored carefully to minimize the recounting of birds at the same or subsequent plots.

Two measures of avian community structure were computed per season (winters or breeding seasons combined) in each area and habitat. These were species richness (S) and abundance (N) of all species combined and of three major foraging guilds. S was the number of species, and N was the cumulative number of contacts (number/10 ha) pooled from all plots within a given area or habitat. The major guilds were trunk-bark foragers (species typically foraging on tree trunks or large branches), ground-shrub foragers (species typically foraging at or < 2 m above ground level), and sallier-canopy foragers (species typically foraging ≥ 2 m above ground level in vegetation) (Yahner 1986). Abundance (number/10 ha) of individual species also was determined per season (winters or breeding seasons combined) as the cumulative number of contacts (number/10 ha) pooled from all plots within a given area or habitat.

I derived an importance value (IV) for each species per season (winters or breeding seasons) as a means of comparing the importance of species to the avian community at the Barrens Grouse HMA (Yahner 1986, Rollfinke and Yahner 1990). IV was calculated as the sum of a relative numerical component (RN) and a relative distribution component (RD). RN was the abundance (total number of contacts) of a given species at the 90 plots pooled from the two winters or the three breeding seasons and divided by the maximum abundance recorded for a species. Maximum abundance was 30 contacts for Black-capped Chickadees in winters and 89 contacts for Common Yellowthroats in breeding seasons ($\times 100$). RD was the proportion of the nine habitats in which a given species was recorded during the two winters or the three breeding seasons combined ($\times 100$). I summed these two components (max. = 200) to arbitrarily categorize a species as being of high ($IV \geq 125$), moderate (50–124), or low importance (≤ 49) in winters or breeding seasons.

I compared observed versus expected abundances of all species combined and of each foraging guild and species among the 0%, 50%, and 75% areas. When sample sizes were adequate, I made comparisons among habitats within a given area, using G -tests for goodness-of-fit (Sokal and Rohlf 1981). Expected abundances were obtained by multiplying the proportion of total number of plots per area or habitat by the cumulative number of contacts of all species, guilds, or species. Similarities in avian species composition among the three areas were examined by indices of proportional similarity (PS) (Brower and Zar 1984), using abundance of each species per area. In all analyses, avian data were pooled by season (two winters or three breedings seasons, respectively) to give a better measure of habitat-use patterns than comparisons between or among years and to increase sample size for statistical analyses (Rice et al. 1984, Yahner 1986).

RESULTS

Wintering Bird Community

Community structure.—Eleven bird species were noted in the three areas at the Barrens Grouse HMA during winters 1987–1988 and 1988–1989, with most ($N =$ seven) species consisting of trunk-bark foragers (Table 1). S and N of all species combined, of trunk-bark foragers, and of ground-shrub foragers were higher in the 50% than in the other two areas. Species composition was more similar between 50% and 75% areas

TABLE 1

SPECIES RICHNESS (S) AND ABUNDANCE (N , NUMBER/10 HA) OF ALL SPECIES COMBINED AND OF TWO MAJOR FORAGING GUILDS IN THREE AREAS OF FOREST CLEAR-CUTTING AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING WINTERS 1987–1988 AND 1988–1989 COMBINED

	Area of forest clear-cutting			
	0% (10) ^a	50% (40)	75% (40)	Total (90)
Species richness, S :				
All species combined	4	10	7	11
Trunk-bark foragers	3	6	5	7
Ground-shrub foragers	1	4	2	4
Abundance, N :				
All species combined	14.0	19.6	12.2	15.7
Trunk-bark foragers	10.5	13.5	9.1	11.2
Ground-shrub foragers	3.5	6.1	3.1	4.5

^a Numbers of 1-ha plots/area are given in parentheses.

($PS = 72\%$) than between either 0% and 50% areas ($PS = 33\%$) or 0% and 75% areas ($PS = 41\%$). For instance, six species occurred in both 50% and 75% areas, whereas only three species occupied both 0% and 50% areas (Table 2).

Abundances of all species combined, of trunk-bark foragers, and of ground-shrub foragers did not vary from expected among the three areas (G 's < 4.1 , $df = 2$, $P > 0.10$). However, abundance of all species combined was significantly different from expected among the four habitats in the 50% area ($G = 25.4$, $df = 3$, $P < 0.001$), being less than expected in both 2-year-old oak and uncut oak bordered by younger clear-cut plots (G 's > 5.5 , $df = 1$, $P < 0.05$) but higher than expected in uncut oak bordered by older clear-cut plots ($G = 19.0$, $df = 1$, $P < 0.001$). Furthermore, abundance of trunk-bark foragers varied among the four habitats in both 50% and 75% areas (G 's > 9.8 , $df = 3$, $P < 0.05$); in each of these two areas, abundance was greater than expected in uncut oak bordered by older clear-cut plots and in uncut aspen, respectively (G 's > 9.8 , $df = 1$, $P < 0.001$).

Population abundance.—Of the 11 wintering species, only the Black-capped Chickadee was of high importance ($IV > 125$), and three species (Golden-crowned Kinglet, American Tree Sparrow, and Ruffed Grouse) were of moderate importance to the bird community ($IV = 50$ – 124) (Table 2). However, the Golden-crowned Kinglet was noted only in winter 1988–1989. Abundances of individual species did not differ from expected among the three areas (G 's > 2.8 , $df = 2$, $P > 0.10$).

TABLE 2
 ABUNDANCE (N = NUMBER/10 HA) OF INDIVIDUAL SPECIES IN EACH OF THREE AREAS OF FOREST CLEAR-CUTTING AND IMPORTANCE COMPONENTS (IV , RN , RD) OF INDIVIDUAL SPECIES IN THREE AREAS POOLED AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING WINTERS 1987-1988 AND 1988-1989 COMBINED

Classification-species ^b	Area of forest clear-cutting				IV	$(RN, RD)^c$
	0% (10) ^a	50% (40)	75% (40)	Total (90)		
High importance:						
Black-capped Chickadee (<i>Parus atricapillus</i>)	1.7	7.0	5.7	5.8	200	(100, 100)
Moderate importance:						
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	7.0	2.2	1.3	2.3	107	(40, 67)
American Tree Sparrow (<i>Spizella arborea</i>)	0.0	1.7	1.7	1.6	83	(27, 56)
Ruffed Grouse (<i>Bonasa umbellus</i>)	3.5	1.7	1.3	1.7	63	(30, 33)
Low importance:						
Hairy Woodpecker (<i>Picoides villosus</i>)	0.0	1.7	0.0	0.8	46	(13, 33)
Tufted Titmouse (<i>Parus bicolor</i>)	0.0	0.9	0.9	0.8	46	(13, 33)
Blue Jay (<i>Cyanocitta cristata</i>)	0.0	2.2	0.0	1.0	39	(17, 22)
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	0.0	1.3	0.4	0.8	35	(13, 22)
Downy Woodpecker (<i>Picoides pubescens</i>)	1.7	0.0	0.9	0.6	21	(10, 11)
Brown Creeper (<i>Certhia americana</i>)	0.0	0.4	0.0	0.2	14	(3, 11)
Northern Cardinal (<i>Cardinal cardinalis</i>)	0.0	0.4	0.0	0.2	14	(3, 11)

^a Numbers of 1-ha plots/area are given in parentheses.

^b Classification of bird species was based arbitrarily on values of IV : high importance, $IV \geq 125$; moderate importance, $IV = 50-124$; low importance, $IV < 49$.

^c Importance components: $IV = RN + RD$; where the relative numerical component, $RN =$ abundance (total number of contacts) of a given species at all plots pooled during the two winters combined and divided by the maximum abundance for a species ($\times 100\%$); and relative distribution component, $RD =$ proportion of habitats in which a species was recorded during the two winters combined ($\times 100\%$).

TABLE 3
SPECIES RICHNESS (S) AND ABUNDANCE (N = NUMBER/10 HA) OF ALL SPECIES COMBINED AND OF THREE MAJOR FORAGING GUILDS IN THREE AREAS OF FOREST CLEAR-CUTTING AT THE BARRENS GROUSE HMA, CENTRE COUNTY, PENNSYLVANIA, DURING SPRINGS 1987–1988 COMBINED^a

	Area of forest clear-cutting			
	0% (10)	50% (40)	75% (40)	Total (90)
Species richness, S :				
All species combined	16	31	28	38
Trunk-bark foragers	5	5	5	6
Ground-shrub foragers	4	15	16	20
Sallier-canopy foragers	7	11	7	12
Abundance, N :				
All species combined ^b	68.6 ^c	69.5 ^c	93.3 ^d	80.0
Trunk-bark foragers	12.8	8.1	7.8	8.5
Ground-shrub foragers ^b	20.9 ^c	44.2 ^c	75.3 ^d	55.5
Sallier-canopy foragers ^b	34.9 ^d	17.2	10.2 ^c	16.0

^a Numbers of 1-ha plots/area are given in parentheses.

^b Observed versus expected abundance varied significantly among areas; $G > 5.99$, $df = 2$, $P < 0.05$; G -test for goodness-of-fit.

^c Observed abundance in this area was significantly less than expected; $G > 3.84$, $df = 1$, $P < 0.05$; G -test for goodness-of-fit.

^d Observed abundance in this area was significantly greater than expected; $G > 3.84$, $df = 1$, $P < 0.05$; G -test for goodness-of-fit.

Breeding Bird Community

Community structure.—Thirty-eight bird species were observed in the three areas at the Barrens Grouse HMA during breeding seasons 1987–1989 (Table 3). See Tables 2 and 4 for scientific names of species mentioned in the text. S of all species combined and of ground-shrub foragers were highest in 50% and 75% areas, whereas S of trunk-bark foragers were similar among areas. S of sallier-canopy foragers was highest in the 50% area. N of all species combined and of ground-shrub foragers were greater in the 75% area than in other areas. Species composition was more similar between 50% and 75% areas ($PS = 64\%$) than between either the 0% and the 50% areas ($PS = 33\%$) or the 0% and the 75% areas ($PS = 26\%$). Abundances of all species combined and of ground-shrub foragers were greater than expected in the 75% area and lower than expected in 0% and 50% areas (Table 3). As in winter (Table 1), abundance of trunk-bark foragers did not vary from expected among areas. Abundance of sallier-canopy foragers differed among areas, being greater than expected in the 0% area and less in the 75% area.

Within the 50% area, abundance of all species combined was greater

than expected in 2- and 12-year-old oak (G 's = 4.9, $df = 1$, $P < 0.05$) but less than expected in uncut oak bordered by older clear-cut plots ($G = 26.4$, $df = 1$, $P < 0.001$). Abundance of trunk-bark foragers was higher than expected in uncut aspen bordered by younger clear-cut plots ($G = 10.4$, $df = 1$, $P < 0.001$) and lower in 2-year-old ($G = 11.3$, $df = 1$, $P < 0.001$). Abundance of ground-shrub foragers also was higher than expected in 2- and 12-year-old oak (G 's ≥ 6.4 , $df = 1$, $P < 0.05$), whereas abundance of this guild was lower in both uncut oak habitats (plots C and D) (G 's ≥ 6.5 , $df = 1$, $P < 0.05$). However, abundance of sallier-canopy foragers did not vary among habitats ($G = 7.5$, $df = 3$, $P > 0.05$).

Within the 75% area, abundance of all species combined was greater than expected in 8-year-old aspen ($G = 5.0$, $df = 1$, $P < 0.05$) and lower than expected in uncut oak bordered by younger clear-cut plots ($G = 5.9$, $df = 1$, $P < 0.05$). Abundances of both trunk-bark and sallier-canopy foragers were lower in 8-year-old aspen (G 's ≥ 4.0 , $df = 1$, $P < 0.05$) versus higher in uncut aspen (G 's ≥ 6.7 , $df = 1$, $P < 0.01$); abundance of sallier-canopy foragers also was lower than expected in 2-year-old aspen ($G = 20.1$, $df = 1$, $P < 0.001$). In contrast, abundance of ground-shrub foragers was greater than expected in 8-year-old aspen but lower in uncut aspen (G 's ≥ 14.1 , $df = 1$, $P < 0.001$).

Population abundance.—Of 38 species observed in the three areas during breeding seasons 1987–1989, four (11%) species were of high importance, and 17 (45%) each were of moderate or low importance (Table 4). The four high-importance species were ground-shrub foragers; three of these species (Common Yellowthroat, Rufous-sided Towhee, and Gray Catbird) were encountered more often than expected in the 75% area and were absent from the 0% area. The remaining high-importance species, the Ovenbird, occurred more often than expected in the 0% area.

Abundances of six species classified as moderate in importance differed from expected among the three areas (Table 4). Three species, each in the ground-shrub foraging guild (Golden-winged Warbler, Field Sparrow, and Chestnut-sided Warbler) were found more often than expected in the 75% area. A sallier-canopy forager, the Red-eyed Vireo, occurred more than expected in the 0% area. Abundances of two trunk-bark foragers, Black-capped Chickadees and Tufted Titmice, differed significantly from expected in the 50% area, with the former species observed less than expected and the latter more than expected.

Within the 50% area, abundances of Common yellowthroats and Gray Catbirds were much greater than expected in 2-year-old oak ($G = 12.5$, $df = 1$, $P < 0.001$) and 12-year-old oak ($G = 16.6$, $df = 1$, $P < 0.001$), respectively. Moreover, these two ground-shrub foragers occurred less

often than expected in both uncut oak habitats (G 's ≥ 4.0 , $df = 1$, $P < 0.05$).

Within the 75% area, abundance of Common Yellowthroats was greater than expected in 8-year-old aspen ($G = 21.4$, $df = 1$, $P < 0.001$) but lower in uncut aspen ($G = 25.5$, $df = 1$, $P < 0.001$). Abundance of Gray Catbirds was greater than expected in 12-year-old aspen ($G = 9.2$, $df = 1$, $P < 0.001$) versus lower in 2-year-old aspen or uncut aspen (G 's ≥ 5.1 , $df = 1$, $P < 0.05$). Ovenbirds more frequently occurred in uncut aspen ($G = 8.3$, $df = 1$, $P < 0.001$) but less often in 2- or 8-year-old aspen ($G \geq 4.8$, $df = 1$, $P < 0.05$). Field Sparrows were noted principally in 2-year-old aspen ($G = 13.7$, $df = 1$, $P < 0.001$) but seldom in uncut aspen ($G = 14.4$, $df = 1$, $P < 0.001$). Furthermore, abundance of Chestnut-sided Warblers was lower than expected in uncut aspen ($G = 12.1$, $df = 1$, $P < 0.001$).

DISCUSSION

Wintering Bird Community

A trend in winter after both second (Yahner 1985) and third cutting cycles at the Barrens Grouse HMA was similarity in avian abundance among the three areas of forest clear-cutting. This supports the contention that wintering bird communities in northerly latitudes may be less sensitive to fragmentation resulting from clear-cutting than breeding communities (Yahner 1985), perhaps because wintering birds often form wide-ranging, interspecific flocks (Yahner 1989). However, a somewhat lower species richness in the 0% area compared to 50% or 75% areas may be due to fewer plots sampled in the 0% area.

Abundance of wintering birds was comparable among the three areas, perhaps because of small sample sizes. However, wintering birds more often occurred in uncut habitats. This tendency for wintering birds to use uncut habitats may be related to selection of favorable microclimatic conditions while foraging (Yahner 1987, Petit 1989). For example, in the 50% area, uncut plots bordered by older clear-cut plots (plot D) may have provided greater protection for birds against winter winds than either clear-cut plots (plots A and B) or uncut plots bordered by younger clear-cut plots (plot C) (Ranney et al. 1981, Saunders et al. 1991).

A second trend in winter subsequent to both second (Yahner 1986) and third cutting cycles at the Barrens Grouse HMA was that the community was comprised mainly of birds in the trunk-bark foraging guild. This guild foraged extensively on rough-barked overstory trees (e.g., *Quercus* spp., *P. rigida*) in uncut habitats in all areas (Yahner 1987); rough-barked trees

TABLE 4

ABUNDANCE (N = NUMBER/10 HA) OF INDIVIDUAL SPECIES IN EACH OF THREE AREAS OF FOREST FRAGMENTATION AND IMPORTANCE COMPONENTS (IV , RN , RD) OF INDIVIDUAL SPECIES IN THREE AREAS OF FOREST CLEAR-CUTTING POOLED AT THE BARRENS GROUSE HMA, CENTRE COUNTRY, PENNSYLVANIA, DURING BREEDING SEASONS 1987-1989 COMBINED

Classification-species ^a	Area of forest fragmentation					IV	$(RN, RD)^b$
	0% (10)	50% (40)	75% (40)	Total (90)			
High Importance:							
Common Yellowthroat (<i>Geothlypis trichas</i>) ^c	0.0 ^d	9.0	16.9 ^a	11.5	189	(100, 89)	
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>) ^c	0.0 ^d	5.8	14.0 ^e	8.8	165	(76, 89)	
Gray Catbird (<i>Dumetella carolinensis</i>) ^c	0.0 ^d	6.9	9.3 ^e	7.1	151	(62, 89)	
Ovenbird (<i>Seiurus aurocapillus</i>) ^c	12.8 ^e	2.3	7.3	5.7	127	(49, 78)	
Moderate importance:							
Black-capped Chickadee ^c (<i>Parus atricapillus</i>)	5.8	1.5 ^d	4.1	3.1	116	(27, 89)	
Wood Thrush (<i>Hylocichla mustelina</i>)	2.3	4.1	1.7	2.8	114	(25, 89)	
Red-eyed Vireo (<i>Vireo olivaceus</i>) ^c	12.8 ^e	2.6	3.5	4.1	114	(36, 78)	
Golden-winged Warbler (<i>Vermivora chrysoptera</i>) ^c	0.0	1.5	5.5 ^e	3.1	105	(27, 78)	
Scarlet Tanager (<i>Piranga olivacea</i>)	7.0	3.2	2.0	3.1	105	(27, 78)	
Field Sparrow (<i>Spizella pusilla</i>) ^c	0.0	2.3	7.3 ^e	4.3	93	(37, 56)	
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>) ^c	0.0	2.3	6.1 ^e	3.7	89	(33, 56)	
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	0.0	3.5	2.3	2.6	89	(67, 22)	
Black-and-white Warbler (<i>Mniotilta varia</i>)	1.2	0.9	2.3	1.6	89	(13, 67)	
Brown-headed Cowbird (<i>Molothrus ater</i>)	4.7	1.5	0.6	1.4	79	(12, 67)	
Tufted Titmouse ^c (<i>Parus bicolor</i>)	3.5	3.8 ^e	0.9	2.5	77	(21, 56)	
Indigo Bunting (<i>Passerina cyanea</i>)	0.0	3.2	2.3	2.5	77	(21, 56)	
Downy Woodpecker (<i>Picoides pubescens</i>)	1.2	1.7	0.3	1.0	73	(9, 67)	
Blue Jay (<i>Cyanocitta cristata</i>)	0.0	3.2	0.9	1.8	72	(16, 56)	
Northern Oriole (<i>Icterus galbula</i>)	1.2	3.2	0.0	1.6	57	(13, 44)	
Eastern Wood-Pewee (<i>Contopus virens</i>)	7.0	1.2	0.3	1.4	56	(12, 44)	
American Goldfinch (<i>Carduelis tristis</i>)	0.0	0.3	2.0	1.0	53	(9, 44)	

TABLE 4
CONTINUED

Classification-species ^a	Area of forest fragmentation					IV	(RN, RD) ^b
	0% (10)	50% (40)	75% (40)	Total (90)			
Low importance:							
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	1.2	1.5	0.0	0.8	51	(7, 44)	
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	0.0	0.6	0.3	0.4	36	(3, 33)	
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	3.5	0.3	1.5	1.2	43	(10, 33)	
Hairy Woodpecker (<i>Picoides villosus</i>)	1.2	0.0	0.3	0.3	24	(2, 22)	
Pine Warbler (<i>Dendroica pinus</i>)	0.0	0.3	0.3	0.3	24	(2, 22)	
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	0.0	1.2	0.0	0.5	16	(5, 11)	
Ruffed Grouse (<i>Bonasa umbellus</i>)	0.0	0.0	0.6	0.3	13	(2, 11)	
Least Flycatcher (<i>Empidonax minimus</i>)	0.0	0.6	0.0	0.3	13	(2, 11)	
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	2.3	0.0	0.0	0.3	13	(2, 11)	
Chipping Sparrow (<i>Spizella passerina</i>)	0.0	0.6	0.0	0.3	13	(2, 11)	
Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)	0.0	0.3	0.0	0.1	12	(1, 11)	
American Crow (<i>Corvus brachyrhynchos</i>)	0.0	0.0	0.3	0.1	12	(1, 11)	
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	0.0	0.3	0.0	0.1	12	(1, 11)	
House Wren (<i>Troglodytes aedon</i>)	0.0	0.3	0.0	0.1	12	(1, 11)	
Worm-eating Warbler (<i>Helmitheros vermivorus</i>)	1.2	0.0	0.0	0.1	12	(1, 11)	
Nashville Warbler (<i>Vermivora ruficapilla</i>)	0.0	0.0	0.3	0.1	12	(1, 11)	
Northern Cardinal (<i>Cardinalis cardinalis</i>)	0.0	0.0	0.3	0.1	12	(1, 11)	

^a Classification of bird species was based arbitrarily on values of IV: high importance, IV \geq 125; moderate importance, IV = 50–124; low importance, IV < 49.

^b Importance components: IV = RN + RD; where the relative numerical component, RN = abundance (total number of contacts) of a given species at all plots pooled during the three breeding seasons combined and divided by the maximum abundance for a species (\times 100%); and relative distribution component, RD = proportion of habitats in which a species was recorded during the three breeding seasons combined (\times 100%).

^c Observed vs. expected abundance varied significantly among areas; $G > 5.99$, $df = 2$, $P < 0.05$; G -test for goodness-of-fit.

^d Observed abundance in this area was significantly less than expected; $G > 3.84$, $df = 1$, $P < 0.05$; G -test for goodness-of-fit.

^e Observed abundance in this area was significantly greater than expected; $G > 3.84$, $df = 1$, $P < 0.05$; G -test for goodness-of-fit.

provided numerous crevices for arthropods, which are important food for wintering birds (e.g., Brawn et al. 1982, Morrison et al. 1985). In nearby (< 10 km) irrigated forests, most wintering birds also were trunk-bark foragers and used rough-barked trees as a preferred foraging substrate (Rollfinke and Yahner 1990, Rollfinke and Yahner 1991).

The Black-capped Chickadee, a trunk-bark foraging species, was the most important wintering species after both second (Yahner 1986) and third cutting cycles. Chickadees typically are abundant in managed, eastern deciduous forests during winter (e.g., Conner et al. 1979, Yahner 1986, Rollfinke and Yahner 1990). In contrast, two other trunk-bark foraging species, the Downy Woodpecker and the White-breasted Nuthatch, were well-represented after the second (Yahner 1986) but not after the third cycle. I attribute this decline in importance of Downy Woodpeckers and White-breasted Nuthatches after the third cycle to a reduction in extent of uncut forest (e.g., see Casey and Hein 1983). Prior to the third cycle, I predicted that abundance of these two species may decline with greater forest clear-cutting at the Barrens Grouse HMA (Yahner 1985). In contrast, Robbins et al. (1989) found that relative abundances of both Downy Woodpeckers and White-breasted Nuthatches were negatively correlated to the amount of forest within a 2-km radius of sampling points in fragmented landscapes of Maryland.

The Golden-crowned Kinglet was scarce after the second cutting cycle (Yahner 1986) but was important to the wintering bird community after the third cutting cycle. I would have expected abundance of this trunk-bark forager to be lowest after the third cycle with additional removal of overstory trees via clear-cutting because Golden-crowned Kinglets generally feed in the upper canopy (Franzreb 1984, Rollfinke and Yahner 1991). However, the warm winter of 1988–1989 may have played a major role in abundance patterns of kinglets subsequent to the third cycle. Mean ambient temperature in January 1989 (-1.0°C) was higher than in January 1988 (-6.5°C) or compared to a normal January (-3.1°C) (Penn State Weather Observatory, University Park, Pennsylvania). Root (1988) observed that abundance of Golden-crowned Kinglets in northerly regions was highest where January temperatures typically remain above freezing.

A third trend in the wintering avian community subsequent to both second (Yahner 1986) and third cycles was a relative lack of ground-shrub foraging species. I suspect that species foraging at or near ground level were uncommon or absent during winter because of a scarcity of weed seeds as a food resource (Yahner 1986). Conversely, in nearby (< 10 km) irrigated forests, seeds of herbaceous vegetation were abundant, thereby resulting in high numbers of wintering ground-shrub foragers, such as

White-throated Sparrows and Northern Cardinals (Rollfinke and Yahner 1990).

Despite the paucity of ground-shrub relative to trunk-bark foraging species in winter, two ground-shrub foragers, the Ruffed Grouse and the American Tree Sparrow, became moderately important ($IV \geq 50$) after the third cutting cycle. Because both grouse and tree sparrows prefer edges or brushy vegetation (Gullion 1977, Root 1988), I attribute this increased importance of the two species to greater availability of early successional vegetation created by clear-cutting in the third cycle. On the treated sector, total percentage of clear-cut plots and, hence, availability of brushy vegetation, nearly doubled from the second (36%) to the third cycle (61%). Moreover, length of edge habitat (i.e., junction of two plots of different age) increased about 2- and 1.5-fold in 50% and 75% areas, respectively, from second to third cycles (Yahner 1992).

Breeding Bird Community

Breeding bird diversity is largely a function of habitat diversity (Roth 1976, Yahner 1986). Hence, greater species richness on the treated than on the reference sector during breeding seasons subsequent to the third cutting cycle was expected with the creation of a checkerboard mosaic of small, different-aged stands via clear-cutting (after Yahner 1984, Thompson and Capen 1988).

Conner et al. (1979) suggested that the effects of forest clear-cutting on avian communities vary with season, seral stage, and bird species. Similarly, I have shown that the influence of extent of forest clear-cutting on avian communities not only differs seasonally (e.g., winter versus breeding season) but also with guilds or bird species (e.g., *S* of trunk-bark versus ground-shrub foragers among the three areas). However, changes in abundance patterns of individual species may not always be related to extent of habitat fragmentation resulting from forest clear-cutting. For example, although abundances of Black-capped Chickadees and Tufted Titmice are reported to differ with degree of fragmentation (e.g., Robbins et al. 1989), abundances of these two species varied from expected in the 50% area (lower in chickadees versus higher in titmice) as a possible consequence of interspecific competition. Survivorship and recruitment of Black-capped Chickadees are lower when chickadees are sympatric with titmice (Loery and Nichols 1985)

Ground-shrub foragers comprised the major guild in the breeding seasons after both second (Yahner 1986) and third cutting cycles. I attribute similarities in species richness of the ground-shrub foraging guild between 50% and 75% areas to the availability of early successional habitats and

associated microenvironments for a variety of bird species (after Willson 1974, Thompson and Capen 1988, Derleth et al. 1989). However, abundance of the ground-foraging guild was higher in the 75% than the 50% area, perhaps because the 75% area contained a greater proportion of clear-cut stands with low-lying, brushy vegetation for nesting and foraging (Yahner 1987, 1991). In particular, the three species with the highest importance to the breeding bird community (Common Yellowthroats, Rufous-sided Towhees, and Gray Catbirds) were most abundant in the 75% area and are adapted to brushy vegetative conditions (e.g., Yahner 1986). Of these three species, the Common Yellowthroat was the most abundant after the third cycle, whereas the Rufous-sided Towhee predominated after the second cycle (Yahner 1986). Common Yellowthroats are one of the best "indicator" species of brushy vegetative conditions (Sedgwick and Knopf 1987). Golden-winged Warblers and Field Sparrows, which were species of moderate importance, were most common in the 75% area; both species are characteristic of brushy, open-canopy habitat (e.g., Casey and Hein 1983, Yahner 1986). I believe that increased numbers of Common Yellowthroats, as well as those of Golden-winged Warblers and Field Sparrows, after the latter cycle, especially in the 75% area, resulted from additional early successional habitat provided by clear-cutting.

Abundances of the sallier-canopy foraging guild and representative species (e.g., Red-eyed Vireos and Eastern Wood-Pewees) were higher on the reference than the treated sector because the reference sector contained extensive closed canopy and relatively open understory for foraging and nesting (e.g., Maurer et al. 1981, Thompson and Capen 1988). Conversely, I attribute greater *S* in the 50% area partially to the occurrence of less abundant sallier-canopy foragers (e.g., Northern Orioles and Cedar Waxwings) in 2-year-old oak habitat (Yahner, unpubl. data). This habitat was characterized by open canopy interspersed with scattered overstory trees ($N = 10\text{--}20$ overstory trees/ha), which were retained by the Pennsylvania Game Commission as "seed" trees in the third cutting cycle.

Two neotropical migrants, Ovenbirds and Red-eyed Vireos, apparently were more sensitive to increased clear-cutting, based on significantly greater abundances in the 0% zone after the third cycle and compared to abundances after the second cutting cycle (Yahner 1986). The impact of forest fragmentation on area-dependent species has been given considerable attention in recent years because of concerns for regional population declines (e.g., Galli et al. 1976, Whitcomb et al. 1981, Robbins et al. 1989). In an earlier study, I proposed that a third cutting cycle could negatively affect the abundance of insectivorous, long-distance migrants (Yahner 1984) that are typical of mature rather than early successional

habitats (e.g., Butcher et al. 1981, Thompson and Capen 1988). Thompson et al. (1992) noted that populations of Scarlet Tanagers and Red-eyed Vireos were reduced in forests managed by clear-cutting compared to mature forests with no recent timber harvest. However, Derleth et al. (1989) found that presence of scattered, small clear-cut stands (1–8 ha) did not have an effect on abundance of various species of forest birds, including Red-eyed Vireos.

Subsequent to the third cutting cycle, I noted a tendency for area-dependent forest birds, such as Ovenbirds, Red-eyed Vireos, and Wood Thrushes, to recolonize and nest in 12-year-old clear-cut habitats in 50% (plot A) and 75% areas (plot A). In contrast, after the second cycle, these species were absent or scarce in clear-cut habitats (≤ 10 -years-old) (Yahner 1986). Thus, any negative effect of increased clear-cutting of small forest stands on abundance and distribution of area-dependent, forest bird species may be short-term; once vegetation in clear-cut stands matures, adequate foraging and nesting sites become available for these species. My current research at the Barrens Grouse HMA is designed to examine the effects of plant succession on avian recolonization of cut habitats on the treated sector with no additional fragmentation via clear-cutting.

I conclude that forest clear-cutting that creates a mosaic of small (1 ha) even-aged stands for Ruffed Grouse habitat does not have a detrimental long-term effect on most species of breeding and wintering forest birds on a localized basis. Moreover, I have observed that nesting success (52%) of breeding birds on the treated sector of the Barrens Grouse HMA was comparable to that reported in other studies conducted in managed or altered landscapes (Yahner 1991).

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